Interpretation of a Discontinuity in the Sense of Verticality at Large Body Tilt

Ronald G. Kaptein and Jan A. M. Van Gisbergen
Department of Biophysics, University of Nijmegen, 6525 EZ Nijmegen, The Netherlands

Kaptein, Ronald G. and Jan A. M. Van Gisbergen. Interpretation of a discontinuity in the sense of verticality at large body tilt. *J Neurophysiol* 91: 2205–2214, 2004. First published December 10, 2003; 10.1152/jn.00804.2003. Results of earlier spatial-orientation studies focusing on the sense of verticality have emphasized an intriguing paradox. Despite evidence that nearly veridical signals for gravicentric head orientation and egocentric visual stimulus orientation are available, roll-tilted subjects err in the direction of the long body axis when adjusting a visual line to vertical in darkness (Aubert effect). This has led to the suggestion that a central egocentric bias signal with fixed strength and direction acts to pull the perceived vertical to the subjects' zenith (M-model). In the present study, the subjective visual vertical (SVV) was tested in six human subjects, across the entire 360° range. For comparison, body-tilt estimates from four subjects where collected in a separate series of experiments. For absolute tilts up to ~135°, SVV responses showed a gradually increasing Aubert effect that could not be attributed to errors in perceived body tilt but was nicely in line with the M-model. At larger absolute tilts, SVV errors abruptly reversed sign, now showing a pattern concordant with errors in body-tilt estimates but incompatible with the M-model. These results suggest that, in the normal working range, the perception of external space and the perception of body posture are based on different processing of body-tilt signals. Beyond this range, both spatial-orientation tasks seem to rely mainly on a common tilt signal.

INTRODUCTION

Spatial orientation requires knowledge about the direction of gravity (e.g., what is up?), which is essential for maintaining upright body posture and for judging visual orientations in space. It is known that tilted subjects make systematic errors when asked to set a visual line to the vertical in an otherwise dark environment. For large roll tilts, beyond 60°, the subjective visual vertical (SVV) typically deviates in the direction of head tilt (Schöne 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000), as if head tilt is underestimated (see Fig. 1*A*). These errors in the judgment of visual orientations, known as the Aubert or A-effect (Aubert 1861), can be quite substantial with peak amplitudes up to 50° for tilts near 130°. For small tilts, errors in the SVV are generally small, although errors opposite to the A-effect, compatible with tilt overestimation, have been reported (Müller or E-effect) (Müller 1916). Yet when subjects are asked to adjust or to estimate their body tilt in space, their performance is typically much better (Mast and Jarchow 1996; Mittelstaedt 1983; Van Beuzekom et al. 2001). The latter finding indicates that a quite reasonable head-orientation in space signal is available. Given this para-

dox, a major challenge in this field is to explain the origin of the patterns of large systematic errors in the SVV task.

Exploring possible mechanisms behind the SVV errors, Mittelstaedt (1983) proposed that an internal bias signal, called the idiotropic vector, plays a crucial role in the SVV computation. In Mittelstaedt's model (M-model for short), a head-fixed vector is added vectorially to a gravity-related signal derived from the otoliths. This bias factor is always aligned with the upward head axis, independent of tilt angle. Accordingly, the additive effect of the idiotropic is to bias the subjective vertical toward this head axis. To justify such a role for the idiotropic in the perception of verticality, the model proposed that imperfections in combining information from the saccule and the utricle, the two otolith organs, cause errors in the head-tilt signal. This nonveridical signal, if uncompensated by the idiotropic, would cause considerable E-effects at small tilts. Thus, the idiotropic vector is seen as a computational strategy to reduce such SVV errors in the commonly used working range of small tilts, at the expense of large A-effects at the rarely encountered large tilts (see Fig. 1, *A* and *B*). Simulations have shown that this model can fit the SVV data in the range 0−180° (e.g., Udo de Haes 1970). The fact that astronauts in space still experience a sense of verticality, even though the otoliths do not provide gravitational information, seems to support this notion of an internal bias signal (Glasauer and Mittelstaedt 1992, 1998; Oman 2003).

The M-model derives body tilt from the otoliths, with no explicit role for the canals. This implies that the important variable for the subjective vertical is final tilt angle and that the direction of rotation, used to get there, is irrelevant. This prediction could not be tested in most previous SVV investigations where the direction of final tilt was coupled to the direction of rotation. In the usual tilting paradigm, the final tilt angle is achieved by the smallest possible rotation from upright, which never exceeds 180°.

In the present study, final tilt angle and rotation direction were uncoupled. We used roll rotations in both directions, with amplitudes up to 360°, to test the SVV at each tilt angle. This was done with two major objectives in mind. Our first goal was to test the M-model prediction that SVV performance is determined by final tilt angle, irrespective of rotation direction. For example, when testing the SVV at a 90° rightward tilt position, will it matter whether this position was reached by a small 90° rightward rotation or by a detour 270° leftward rotation, both starting from upright? An earlier investigation of this issue, with a similar tilting paradigm, yielded mixed results

Address for correspondence: Ronald G. Kaptein, Department of Biophysics, University of Nijmegen, Geert Grooteplein 21, 6525 EZ Nijmegen, The Netherlands. (Email: ronaldk@mbfys.kun.nl)
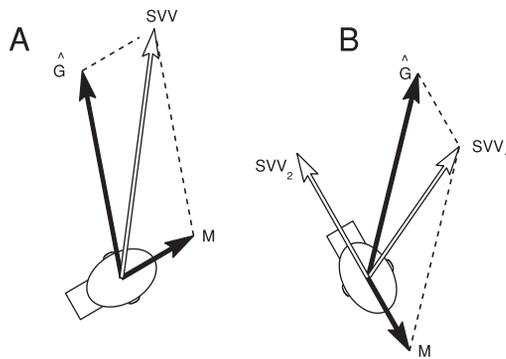
FIG. 1. The subjective visual vertical (SVV) as a compromise between a gravicentric signal and a head-fixed bias signal. *A*: illustration of A-effect in 60° rightward tilted subject seen from behind. Note that line setting is biased toward the head. To explain this, Mittelstaedt's theory proposes that the SVV is the resultant of a normalized gravity signal $\hat{G}$ and a central bias signal, known as the idiotropic vector **M,** which is directed along the head's z axis. In this schematic example, $|\mathbf{M}| = 0.4$. Note that $\hat{G}$ is not precisely aligned with the true direction of gravity due to imperfect fusion of utricle and saccule information ($S = 0.6$; see *Modeling results* for more details). *B*: at 150° tilt the SVV setting predicted by the model (marked SVV_1) again shows an A-effect. In this tilt range, Udo de Haes and Schöne (1970) have noticed an alternative SVV response (marked SVV_2), where the luminous line is set near the body midline. The present experiments have shown an abrupt transition from the first to near the 2nd response mode when tilt exceeds a critical threshold.

(Udo de Haes and Schöne 1970). These authors found a clear effect of rotation direction for large final tilts but none at small tilts. Our second objective was to find out whether quantitative investigation would confirm earlier qualitative descriptions of bistable SVV settings (see Fig. 1*B*) at large tilt angles (Fischer 1930; Udo de Haes and Schöne 1970). The M-model does not predict such bistability effects. Because the earlier reports on this phenomenon have been largely ignored, in spite of its potential importance for spatial-orientation models, we decided that a thorough investigation was warranted.

With regard to our first question, the results appear fully in line with the M-model in the sense that the direction of the preceding rotation had hardly any effect on SVV performance. However, when seen from the perspective of the bistability issue, our SVV results were not predicted by the M-model. In contrast to the earlier studies that formed the basis for this model, we find two different SVV response modes in adjacent tilt regions. The transition from one mode to the other shows indications of bistability, reminiscent of previous reports using a similar tilting paradigm (Fischer 1930; Udo de Haes and Schöne 1970). Verbal estimates of body tilt, collected across the same range, showed no sign of a similar transition between two modes.

In line with earlier results, the pattern of systematic SVV errors characterizing the first response mode was compatible with M-model predictions and could not be attributed to errors in perceived body tilt. By contrast, the second mode of SVV responses, at large tilts, clearly violated the M-model and indicated strong reliance on perceived body tilt.

METHODS

Vestibular roll rotation

The subject was seated in a computer-controlled vestibular stimulator. Body tilt was controlled by rotation about the nasooccipital roll axis at a constant velocity of 30°/s. Roll position was measured using

a digital position encoder with an angular resolution of 0.04°. The cyclopean eye was aligned with the axis of rotation by adjusting the subject's seat in height. The subject's trunk was tightly fixated using seat belts and adjustable shoulder and hip supports. The legs and feet where restrained by Velcro straps. The head was firmly fixated in a natural upright position for looking straight ahead using a padded helmet.

In all experiments, rotation started from the upright position and alternated between clockwise (CW) and counterclockwise (CCW) to a final tilt angle between 0 and 360°. The final rotation angles were randomly chosen at 30° intervals (0, 30, 60,. . ., 330, 360°), but some scatter (range: ±10°) was deliberately superimposed. For some subjects, intermediate tilt angles (at 15° intervals) in the range 90−270° were added. Before experiments, subjects were informed about the 360° testing range. Before testing began, subjects were given a few practice trials to get used to the experimental paradigm.

After a rotation to a certain tilt angle, there was a 30-s waiting period before testing began to allow most of the postacceleration effects in the semicircular canals to subside. After a trial, subjects returned to the upright position where they remained for 60 s, with the room lights on. Vision was always binocular, and subjects were allowed to move their eyes freely. Subjects gave their informed consent before participating in the experiments and were told that they could terminate the experiment at any time. Subjects never received feedback about their performance.

Experiments

Spatial orientation was tested in two different tasks in separate series of experiments.

SUBJECTIVE VISUAL VERTICAL (SVV) PARADIGM. The SVV experiments were performed using a uniformly illuminated line with an angular subtense of 20° mounted at a distance of ~90 cm in front of the subject. The rotation axis of the line coincided with the roll axis of the subject. The line was polarized by a bright dot at one end, creating the appearance of an exclamation mark. Before the experiment began, the subject was instructed that the line should be set parallel to the direction of gravity, with the bright dot pointing to the ceiling. The line could be set with an angular resolution of ~0.5°.

After the 30-s waiting period, the line was switched on in a random orientation and the subject had to adjust the luminous line within 30 s. This alignment was done by verbal instructions from the subject about the desired change in line orientation (leftward or rightward) to the experimenter, who rotated the line slowly in the requested direction by computer control. When the subject was finally satisfied with the orientation of the line, typically after several back and forth adjustments, it was switched off and the subject was rotated back to the upright position. Trials where the subject failed to decide on a final setting within 30 s were discarded and repeated later. Six healthy subjects aged 23–59 yr (all males) participated in this paradigm. Three of the subjects were naive. On average, three sessions of ~45 min on different days were needed to collect the data from each subject.

SUBJECTIVE BODY-TILT (SBT) PARADIGM. After the 30-s waiting period, a beep signal prompted the subject to report his body tilt using a clock scale, as if his body were the minute hand (Van Beuzekom and Van Gisbergen 2000). The verbal responses were written down and recorded on audio tape to allow checking afterwards. Four of the subjects (aged 23–59 yr, 1 naive) that participated in the SVV task also took part in this paradigm. On average, two to four sessions of ~45 min on different days were needed to collect the data from each subject.

Data analysis

Tilt position, ρ, was defined as indicated in Fig. 2, *A* and *B*. Thus all possible tilt angles were represented as positive numbers along an

incremental scale from 0 to 360° with $\rho = 0°$ denoting the upright position. One objective of the experiments was to assess how performance in the spatial-orientation tasks, at a given tilt position, depended on whether that particular ρ angle was reached by a CW or a CCW rotation from upright. To prevent misunderstandings, it should be emphasized that ρ denotes final angular head position and has nothing to do with the direction and the amplitude of chair rotation ($\Delta\rho$) required to get there starting from upright. For example, the head position depicted in Fig. 2A will always be denoted as $\rho = 120°$, irrespective of whether the preceding chair rotation was 120° CW or 240° CCW.

When presenting the data, it is sometimes useful to consider the degree of tilt as the deviation from upright on a $0-180°$ scale. In these cases, we will use the term absolute tilt. In figures illustrating tilt-dependent responses (for example, Fig. 3), the horizontal axis will be double-labeled, using both the ρ scale for head tilt ($0-360°$) and the measure for absolute tilt ($0-180°$). On the absolute-tilt axis, 90R and 90L indicate 90° right-ear down and 90° left-ear down, respectively.

RESPONSE ERROR IN SVV TASK. Response error in the SVV task (γ) was defined as the angular difference between the luminous line setting and the real vertical (see Fig. 2, A and B). Errors in the clockwise direction, seen from behind the subject, were taken positive (see Fig. 2A). As a consequence, an A-effect during rightward tilt (as in Fig. 2A) yields a positive γ value. A-effects during leftward tilt ($\rho > 180°$, as in Fig. 2B) are expressed as negative γ values.
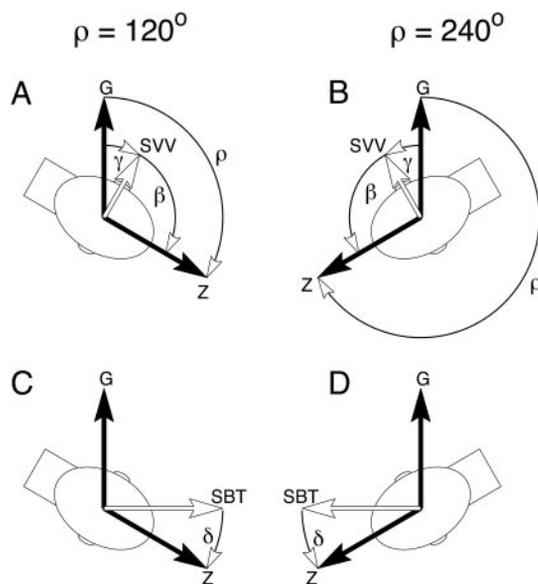
FIG. 2. Explanation of angular definitions with subject in rear view. The final tilt position of the head (ρ) was defined as the angle between the direction of the physical vertical (G) and the subject's positive z axis (Z). Direction of vestibular rotation was defined as seen from behind the subject. Accordingly, clockwise (CW) rotation, starting from upright, caused right-ear down movement; counterclockwise (CCW) rotation corresponded to left-ear down movement. Note that each final tilt position (ρ) could be reached by a CW as well as a CCW chair rotation, starting from upright. Also notice that $\rho = 360°$ denotes the upright position, reached after a full-round rotation. A and B denote our definition of response error (γ) in the SVV task, which was taken as the angular separation between the required response (G) and the actual setting (SVV) as indicated. Both examples show an A-effect. Parameter β is defined as the angle between the line setting and the subject's z axis. Perfect task execution would imply $\beta = \rho$. C and D illustrate our definition of response error (δ) in the subjective body-tilt paradigm (SBT). Here, error is defined as the actual (Z) minus the reported tilt angle. Both schematic examples show tilt underestimation. This definition allowed us to investigate possible relations between δ and γ. For example, if the A-effect shown in B is caused by the tilt underestimation in D, the 2 errors will be equal. The 2 illustrated tilt positions correspond to $\rho = 120°$ (A and C) and $\rho = 240°$ (B and D).
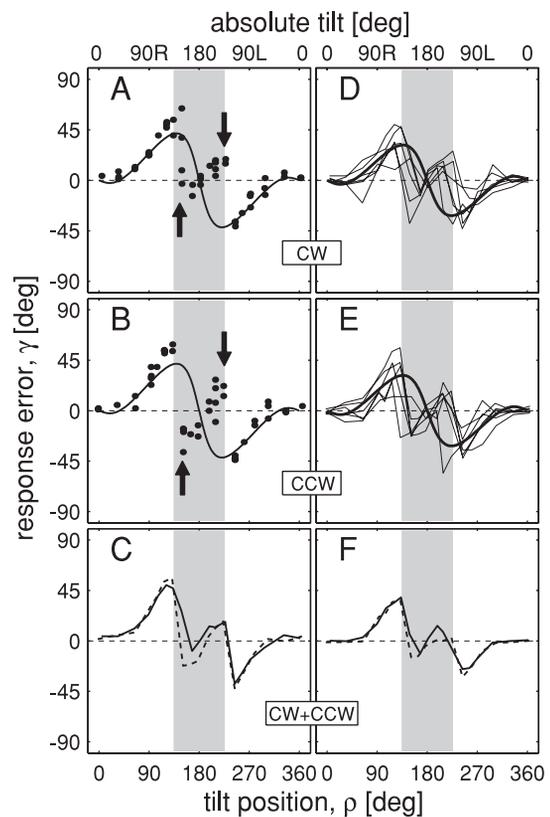
FIG. 3. SVV error profiles. In this and following figures, the horizontal axis is doubly labeled. The bottom scale denotes final tilt position as defined in Fig. 2. The labeling of the horizontal axis at the top denotes absolute tilt angle, the deviation from upright. A and B: SVV errors (γ) from a representative subject (JG) across the full range of possible final tilt angles. Responses obtained after opposite chair rotations from upright are shown separately (CW in A, CCW in B). For example, the data at 90° rightward tilt in A were collected after a 90° CW rotation. The data for the same 90° rightward tilt in B were collected after a 270° CCW rotation. In the white tilt zones, which extend up to 135° absolute tilt, there is a gradually increasing A-effect which can be fitted quite well by the M-model (black curve in A and B, $M = 0.45 \pm 0.04$; $S = 0.6 \pm 0.1$; $R^2 = 0.89$). For an explanation of the Mittelstaedt model and its parameters, see DISCUSSION. The extrapolated best-fit curve for the white zone data does not account for the sudden collapse of the A-effect and the emergence of the E-effect (arrows) at still larger tilts (gray zone). The E-effect at large tilt roughly resembles response mode SVV_2 in Fig. 1. C: the mean error profiles computed from the data in A and B (CW: solid line; CCW: dashed line). When the SVV was tested at small absolute tilts, the responses were virtually identical in CW and CCW trials. There were only small hysteresis effects at large absolute tilts. D and E: thin lines indicate mean error from all six subjects as a function of final tilt angle, sorted by direction of preceding chair rotation (CW in D, CCW in E). The bold lines represent the M-model curve fitted on the population data in the white zone. The fit is very good for the white zone ($M = 0.32 \pm 0.02$, $S = 0.61 \pm 0.03$, $R^2 = 0.70$), but its extention fails to account for the data in the gray zone. The collapse of the A-effect and the emergence of the E-effect at large tilt is typical of most subjects and can still be recognized in the population average. F: mean population profiles for CW (solid line) and CCW (dashed line). Hysteresis is minimal, just as in C.

RESPONSE ERROR IN SBT TASK. Response errors in the SBT task, to be denoted by δ, were defined as the angular difference between the real and the reported body-tilt angle (see Fig. 2, C and D). Errors in the clockwise direction, seen from behind the subject, were taken positive (see Fig. 2C). This definition makes it easy to check for the possibility that A- and E-effects in the SVV task may simply be a reflection of errors in the SBT task. If this were the case, the two tilt-dependent error profiles [$\gamma(\rho)$ and $\delta(\rho)$] should be similar.

MODEL FITS AND STATISTICAL ANALYSIS. The fits in the DISCUSSION were obtained with the least-squares method, using the Nelder-

Mead minimization algorithm as implemented in the routine fminsearch (Matlab 6.0; The Mathworks), in combination with a multistart procedure using different initial parameters. Standard deviations of the optimal parameters were obtained with the bootstrap method (Press et al. 1992). The Wilcoxon rank-sum test was used for testing CW-CCW differences (hysteresis) in the SVV and SBT paradigms. A linear regression was used to investigate a possible relation between the errors in the SVV and the SBT tasks. Statistical results were considered significant if $P < 0.05$. Because the tested tilt positions of the SVV and SBT tasks were not everywhere identical, a few tilt angles could not be included in the correlation analysis.

RESULTS

The present study has investigated two aspects of spatial orientation in roll-tilted subjects across the entire $0-360°$ range. First, we determined the SVV at many static tilt angles reached by either CW or CCW chair rotation. Second, verbal estimates of subjective body orientation in space were collected in the same conditions in separate experiments.

Subjective visual-vertical task

COLLAPSE OF THE A-EFFECT AT LARGE ABSOLUTE TILTS. According to classical descriptions of the SVV (for reviews, see Howard 1982, 1986; Van Beuzekom and Van Gisbergen 2000), A-effects show a gradual increase for absolute tilts beyond $\sim60°$, a peak near $130°$ tilt, and a smooth decay back to zero at $180°$ tilt. Based on this account, the expected result for the $0-360°$ tilt range is a biphasic curve with a positive section for rightward tilts ($0-180°$) and a symmetrical negative section for leftward tilts ($180-360°$). The actual data, however, show a more complex pattern. Figure 3 (*left*), showing the CW and CCW data from one subject in separate panels, conforms with the classical picture for absolute tilts up to $\sim135°$ but also shows clear deviations for large absolute tilts near upside down (135–180°).

The gray zone in Fig. 3 highlights the tilt range ($135-225°$) where the response pattern deviates from the classical picture. To illustrate this, the M-model was fitted to all data outside the gray zone. This curve, which qualitatively conforms to the classical results, is shown in Fig. 3, *A* and *B*. It is clear that for absolute tilts below $\sim135°$, the data are consistent with the expected increase of the A-effect. For large tilts, however, we see a sudden collapse with clear hints of a transition to an E-effect on either side of the inverted position (indicated by the arrows). It is worth noticing that previous testing of the same subject with chair rotations in a smaller range ($\Delta\rho = 0-180°$) never showed the collapse phenomenon.

Comparison of the mean CW and CCW results (Fig. 3*C*) reveals only minute differences for absolute tilts $<135°$ (white zone). For larger tilts (gray zone), the SVV settings at a given tilt angle sometimes depended on the preceding rotation direction. Even so, the large-tilt E-effect is visible in both CW and CCW trials.

Figure 3, *D* and *E,* shows the results of all subjects for CW and CCW rotations. For small absolute tilts $\leq60°$, two of six subjects show small but clear E-effects, whereas the other four show veridical responses or small A-effects. For medium tilts ($60-135°$), we see the expected gradual increase of the A-effect in all subjects, which is again captured by the M-model. The collapse of the A-effect at larger absolute tilts is visible in five of the six subjects. The solid and dashed thick lines in Fig.

3*F,* showing the averaged data of all subjects, again clearly depict the collapse phenomenon in both CW and CCW data.

Our finding of E-effects at large tilts confirms and quantifies earlier anecdotal reports by Udo de Haes and Schöne (1970). Our data show that the phenomenon is typical and robust in both naive and nonnaive subjects. Furthermore, it appears that the effect is expressed at tilt angles closely adjacent to the inverted position, both in CW and CCW trials.

Udo de Haes and Schöne (1970) suggested that the finding of E-effects at large absolute tilts might be linked to their finding of large hysteresis effects at the same tilt angles. A comparison of CW and CCW results (Fig. 3, *C* and *F*) shows that the mean SVV at a given final tilt angle is virtually independent of the preceding direction of rotation, except for very large tilts. A Wilcoxon rank-sum test on the pooled data of all subjects revealed no significant CW-CCW differences except for one tilt position ($\rho = 198°$) near upside-down.

Body-tilt estimation task

Figure 4, *A* and *B,* shows the data of the body-tilt estimation task for the same subject as in Fig. 3, *A* and *B*. Mean errors are small (Fig. 4*C*) and show no convincing overall resemblance with the errors in the SVV task (Fig. 3). The other three subjects tested with this paradigm show roughly the same behavior. Figure 4, *D* and *E* (thin lines), shows the mean results of all four subjects for CW and CCW rotation together with the population mean (bold line). Systematic errors are generally smaller than in the SVV paradigm.

In all subjects, small systematic errors are seen that can be described most parsimoniously as a underestimation of the total rotation ($\Delta\rho$). For example, for a real $360°$ rotation, the sensed rotation, implied by the subject's estimate of final body tilt, is always $<360°$. These hysteresis effects are clearly visible in Fig. 4*F,* where the CW and CCW pooled-data means of all subjects are shown. A Wilcoxon rank-sum test on the pooled data of all subjects indeed revealed significant differences for the majority of tilt positions.

Comparison of errors in the two spatial-orientation tasks

To investigate a possible relation between the SBT and the SVV results, we compared the population means of the four subjects that were tested in both paradigms. The result can be seen in Fig. 5. The immediate overall impression is that the pattern of systematic errors in the two tasks is strikingly different. However, instead of merely confirming earlier reports about a dissociation of performance in the two spatial-orientation tasks (see INTRODUCTION), our results suggest radically different pictures in the white and the gray zone. In the white zone, our results provide strong additional evidence in favor of dissociation. Previous studies, which only used direct rotations toward the final tilt angle (i.e., $\Delta\rho \leq 180°$), have contrasted the large errors in the SVV task (A-effect) in the medium tilt range with the typically small systematic errors in subjective body tilt. Our direct rotation results support this picture (see left-hand white zone in Fig. 5*A* and right-hand white zone in Fig. 5*B*). In the other white zones, representing the data collected at final tilts reached by indirect rotations ($\Delta\rho > 180°$), the dissociation is even more convincing. Here it is obvious at all final tilt angles, even at small absolute tilts
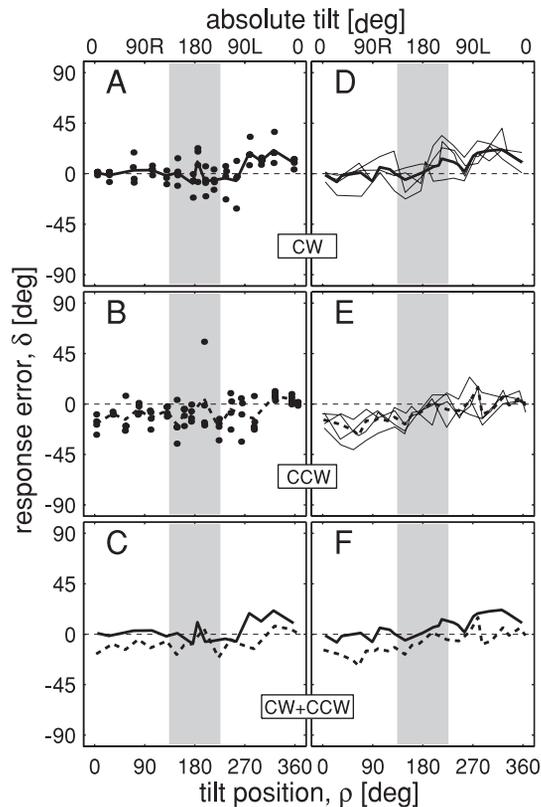
FIG. 4. Subjective body-tilt (SBT) task results. *A* and *B*: SBT errors (δ) from the same subject as in Fig. 3 across the full range of possible final tilt angles. Responses obtained after opposite chair rotations from upright are shown separately (CW in *A*, CCW in *B*). Overall, there are no indications of a tilt-dependent pattern of errors resembling the SVV results. *C*: mean error profiles computed from the data in *A* and *B* (CW: solid line; CCW: dashed line). Unlike in the SVV results, hysteresis effects are not negligible nor limited to large final tilt angles. *D* and *E*: thin lines show mean error in SBT task from all 4 subjects as a function of final tilt angle, sorted by direction of preceding chair rotation (CW in *D*, CCW in *E*). Bold lines in each panel show corresponding population means. Note that systematic errors are small without any sign of an abrupt transition at the boundary between the white and the gray tilt zone. Differences between responses in CW and CCW trials may indicate partial reliance on path integration. *F*: mean population profiles for CW (solid line) and CCW (dashed line), with a clear suggestion of hysteresis. Unlike the situation in the SVV experiments, these effects are most convincing at small absolute tilts.

(Fig. 5, *A* and *B*). Interestingly, the uncoupling seen after a full-cycle rotation back to upright ($\Delta\rho = 360°$) is now due to SBT errors rather than SVV errors. Taken together, our results show a very clear dissociation of SVV and SBT performance across the entire white zone tilt range. Remarkably, this disparity in task performance is not upheld in the gray tilt zone. After the collapse of the A-effect, errors in the subjective vertical task closely approximate those in the perception of body tilt. This coupling is particularly striking in the CCW range (Fig. 5*B*).

To investigate these relationships further, we performed separate linear regressions for the white and the gray zone (see Fig. 6, *A* and *B*). A problem with this analysis in the gray zone was the bistable nature of SVV responses in the transition region. Because we wished to characterize the large-tilt data after the collapse of the A-effect, we excluded SVV data points in the gray zone with A-effects >40°. This ruled out 8 of the 80 data points. Based on the individual means from each of the

four subjects, the correlation between SBT error and the corresponding SVV error in the white zone (Fig. 6*A*) is not significant ($r = -0.16$; $P = 0.17$; $n = 74$). For the gray zone, however, the correlation is highly significant ($r = 0.51$; $P = 0.003$; $n = 31$). In the case of a one-to-one relation between errors in the two spatial orientation tasks, the data points would scatter around a line with unity slope. The actual slope (0.6 ± 0.1) is somewhat smaller (Fig. 6*B*).

DISCUSSION

Overview

Testing both the subjective vertical and the sense of body tilt, we assessed spatial orientation performance at static tilt angles across the entire range. Roll tilts ranging from 0 to 360° were applied in either direction (CW and CCW) so that there was no relation between rotation direction and final tilt position. In the first part of this section, our main experimental findings will be compared with those of previous studies. In the second part, we clarify why the widely accepted M-model cannot account for our new findings and present an alternative scheme.
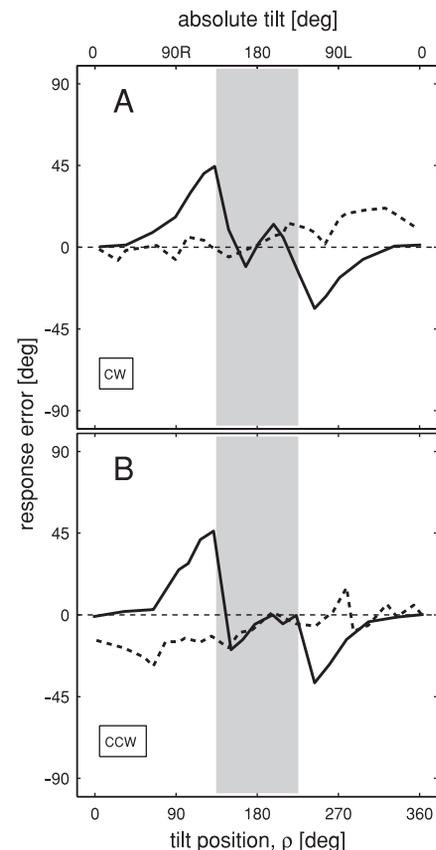

FIG. 5. Comparison of performance in the 2 spatial orientation tasks. Comparison of the population means for SVV (—) and SBT results (- - -), from the 4 subjects that were tested in both paradigms. Results from CW (*A*) and CCW (*B*) rotations are shown separately. The overall pattern of errors is clearly different in the 2 tasks, and SBT errors are generally smaller than SVV errors. However, comparison of results at large tilts (gray zone), shows a strong similarity between SBT and SVV errors.
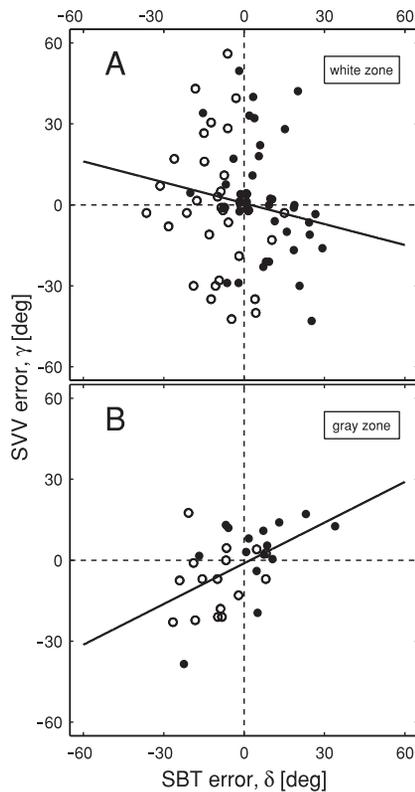
FIG. 6. Correlation between SBT and SVV errors at large tilts. *A*: corresponding SBT and SVV errors, based on individual means from each of the 4 subjects, for the white zone. No significant correlation between SBT and SVV errors was found ($r = -0.16$; $P = 0.17$; $n = 74$). *B*: same analysis as in *A* for the gray zone. The correlation between SBT and SVV errors is now highly significant ($r = 0.51$; $P = 0.003$; $n = 31$). The slope of the linear regression line is 0.6 ± 0.1. ●, CW data; ○, CCW data. The horizontal shift (CW vs. CCW) of the SBT data points reflects the hysteresis effect seen in Fig. 4*F*. Bold lines show the results of the linear regression.

Main experimental findings

UNEXPECTED E-EFFECT AT LARGE TILT. In the tilt zone ≤135°, marked white in Fig. 3, all subjects showed the response pattern expected from the literature, with only minor A- or E-effects at small tilts and a steadily increasing A-effect for larger tilts. Between 135 and 150° absolute tilt, however, we failed to see the gradual decline in the A-effect described in the literature (see e.g., Udo de Haes 1970). Instead, the errors in this range suddenly changed sign from large A-effects to clear E-effects (see Fig. 3). This transition was seen in five of six subjects and occurred in both naive and nonnaive subjects.

Previous reports (Fischer 1930; Udo de Haes and Schöne 1970) have provided fragmentary descriptions of SVV settings in the same tilt range, which point in the same direction. Both papers mention that subjects had difficulties in setting the line when tilted almost upside down because two different responses seemed equally acceptable to them. One mode involved the usual A-effect as reported in other investigations, the other resembled an SVV setting approximately along the symmetry plane of the body (see Fig. 1*B*).

Udo de Haes and Schöne (1970) state that the "egocentric SVV settings" were more prevalent when the near-inverted position was reached after a detour rotation passing through the 180° position instead of by the shorter direct rotation in the opposite direction. Such a difference was not seen in our data:

the sudden transition from A- to E-effect was present in both CW and CCW data for the same final tilt angle (see Fig. 3).

The obvious question remains why the A-to-E-effect transition was not seen in most of the earlier work on the SVV. To begin with, it is clear that the phenomenon will be missed by studies with a limited tilt range. Even studies covering a large range may still fail to see the sharp transition when using coarse sampling at large tilt angles. The rotation paradigm may also affect the outcome for less trivial reasons. As a common element with the present study, it is striking to note that two earlier reports where a similar phenomenon was briefly mentioned (Fischer 1930; Udo de Haes and Schöne 1970) also rotated subjects across the entire 360° range. It is conceivable that this large range has limited the possibility of using prior knowledge provided by relying on a range effect. If subjects know that they will not be rotated beyond 180°, this may affect their judgments. This might explain why the transition phenomenon generally did not occur in experiments using a more limited range of chair rotations [for review, see Van Beuzekom and Van Gisbergen 2000; for an exception, see Mast 2000]. Comments from several subjects concerning the nature of the SVV task at large tilt further suggest a possible involvement of cognitive factors. In the tilt range roughly corresponding to the first domain, task execution was more or less automatic. This quality was lost in the second domain where the task was seen as quite difficult. In such a situation, subtle cues may become critically important.

E-EFFECT IS DISTINCT FROM HYSTERESIS. By comparing SVV settings in CW and CCW trials at each tested tilt angle, the available data allowed us to check for the presence of hysteresis. To minimize such effects, our measurements started after a 30-s waiting period so that the aftereffects of the canals could wear off. For reasons that are not well understood, Udo de Haes and Schöne (1970) found that aftereffects may last considerably longer, especially for large absolute tilts. Their report further suggests that the emergence of E-effects at large tilts and hysteresis effects might be linked.

As predicted by the M-model, our data show very little evidence for hysteresis effects. Our findings are in line with Udo de Haes and Schöne (1970) in the small tilt range, where both studies agree that hysteresis is negligible. At large tilts, however, they found clear hysteresis effects whereas our results show only minor CW-CCW differences. Because the E-effect in our data may be robust even when the hysteresis effect was absent (Fig. 3), we conclude that the two phenomena are not tightly linked.

SVV PERFORMANCE AND SENSE OF BODY TILT. The body-tilt estimates (Fig. 4) were collected in separate experiments to explore the possibility that errors in the SVV task might simply reflect errors in tilt perception. Performance in the SBT task was certainly not veridical, but systematic errors were clearly smaller than in the SVV experiments (see Fig. 5), and overall showed a different pattern of tilt dependence. Near the upright position, subjects made only small systematic errors. However, when returning to upright after a 360° rotation, they tended to underestimate the amount of rotation ($\Delta\rho$). This raises the question of whether the body-tilt estimates were partly based on path integration of canal signals, which, because of the high-pass characteristics of this system, will partly decay during the constant velocity rotation. To account for the body-tilt

data on this basis would require a high-pass filter time constant of at least 60 s. Because this is much larger than the time constant of the canals, even when allowing for velocity storage (Mergner et al. 1996), we conclude that the SBT data provide no evidence for an important canal contribution. Notwithstanding recent evidence for expression of canal signals in the subjective vertical (Jaggi-Schwarz and Hess 2003; Jaggi-Schwarz et al. 2003; Pavlou et al. 2003), our SVV results showed even less evidence for canal effects.

Interestingly, a closer look at the data (Fig. 5) confirmed that the SVV and SBT errors vary independently in the white zone (Fig. 6A) but revealed that they are clearly correlated in the gray zone (Fig. 6B). Previous studies (Jaggi-Schwarz and Hess 2003; Mittelstaedt 1983; Van Beuzekom and Van Gisbergen 2000; Van Beuzekom et al. 2001) have suggested that errors in the estimation of body tilt cannot explain the SVV errors. Also clinical evidence (Karnath et al. 2000) suggests that distinct neural systems seem to be involved in these two tasks. Our data confirm this dissociation for small and medium absolute tilts ($\leq 135°$) but not for large tilts. A model attempting to explain how this loss of dissociation and the collapse of the A-effect at large tilt may be connected will be discussed in the next section.

Modeling results

PERFORMANCE OF EXISTING MODELS. Mittelstaedt (1983) was the first to propose that the SVV reflects a compromise between a gravity signal from the otoliths and a head-fixed bias signal, called idiotropic vector (**M**). According to this scheme, the idiotropic is not involved in body-tilt estimates.

In its simplest form, the M-model can be represented as

$$\tan(\beta) = \frac{\dfrac{G \cdot \sin(\rho)}{N}}{\dfrac{S \cdot G \cdot \cos(\rho)}{N} + M_z} \quad (1)$$

Here, ρ is the tilt position and β is the angle between the SVV and the z axis of the body (see Fig. 2). M_z is the size of the head-directed component of the idiotropic vector (**M**) and G represents the magnitude of gravity. The internal representation of the gravity vector in the M-model is normalized by N, so that the size of the idiotropic vector (typically thought to be about 0.4) is a direct indication of the relative strength of these two signals. S is the ratio of the gains of the saccule and the utricle in the fusion process yielding the gravity signal. In the ideal case ($S = 1$), implying a veridical gravity signal from the otoliths, the system would work perfectly at all tilts without any need for the idiotropic vector. When S is too small, as assumed in the model, relying solely on the otoliths would cause errors of the E-type in the important working range of small tilts. The M-model proposes that the functional role of the idiotropic vector is to mitigate these effects in the important small tilt working range, at the cost of an Aubert effect at large tilts (Fig. 1, *A* and *B*).

Hence, our finding of an E-effect at near-inverted positions is incompatible with the original formulation of the M-model. The best-fit curve of the M-model for the entire tilt range, computed from the pooled data, shows this very clearly (Fig. 7A). The best-fit parameter values in Table 1 yield a poor compromise with a low R^2 value as a result.
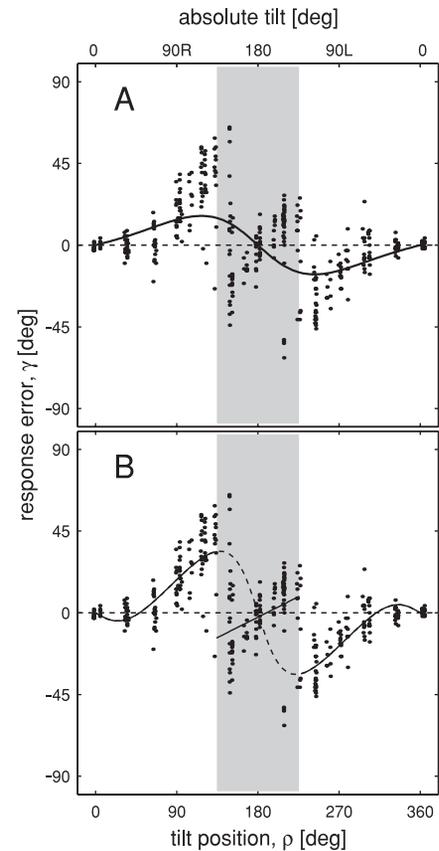

FIG. 7. SVV fit results of M-model and DM-model. *A*: M-model fit to pooled CW and CCW data from all subjects. Note that the model cannot simultaneously account for the A-effect in the white zone and the E-effect in the gray zone. *B*: dual-mechanism model, incorporating different mechanisms for the 2 tilt zones, accounts for A-effect in white zone and E-effect in gray zone. The curved line represents the best-fit result of mechanism 1 (M-model), operating in the white zone. The straight line in the gray zone, representing predicted SVV settings of system 2 based on perceived body tilt (*Eq. 2*), slightly underestimates the E-effect in the data. See text for further description. Best-fit parameter values and the goodness of fit for the 2 models are listed in Table 1. In both fits, all data points were taken into account ($n = 366$).

Eggert (1998) has formulated an interesting reinterpretation of the M-model based on a Bayesian approach. In this model, the visual vertical depends on otolith signals and on an assumed a priori probability distribution of body-tilt angles (the prior). This prior distribution is a Gaussian-like function which peaks at zero tilt. Use of this prior, i.e., by taking into account that large tilt angles are unlikely, allows the system to improve its overall performance in the presence of noisy otolith signals. Interestingly, it can be shown that narrowing the width of the prior distribution can mimic the effect of increasing the strength of the idiotropic vector in the M-model. What makes Eggert's model particularly interesting in the present context is that it can give rise to a bistable SVV signal at large tilts according to a pattern that depends on the prior and the assumed noise characteristics of the otoliths. Like the M-model, this scheme can readily account for the white-zone data. Interestingly, with different parameters, the model can also mimic certain features of the discontinuity in SVV settings in the gray zone. Unfortunately, we have not been able to find a single set of model parameters that could account for the entire data set. Because more definite evaluation of this model would require extensive simulations, far beyond the scope of the

TABLE 1. *Best-fit parameter values of the two spatial orientation models*

Model	Parameter	Best-Fit Value	R^2
M	M_z	0.25 ± 0.02	0.28
	S	0.92 ± 0.04	
DM	M_z	0.33 ± 0.02	0.55
	S	0.58 ± 0.03	
	ρ_c	133 ± 2	

The goodness-of-fit measure R^2 confirms what was already obvious from Fig. 7. The M-model fits poorly, and the DM-model is a major improvement. Adjusted R^2 were also calculated to correct for the number of fit parameters. Because the resulting values are hardly smaller than the R^2, they are not included here. Values are means $\pm$ SD.

present study, caution against premature conclusions is warranted. Nevertheless, even if it appears possible to explain the entire set of SVV responses as the coherent expression of a single mechanism, the question would still remain how to account for the remarkable similarity of performance in the two spatial-orientation tasks (SVV and SBT) emerging at large tilt. Because this seems a daunting requirement for a single mechanism, we proceed to explore the possibility that actually two different computational strategies, embodied by distinct mechanisms, may be responsible for the discontinuity in SVV settings.

DIFFERENT COMPUTATIONAL STRATEGIES IN THE TWO TILT ZONES. As we saw earlier, there is nothing wrong with the M-model in the white tilt zone (see Fig. 3, *D* and *E*). However, there are several indications that the brain shifts to a different computational strategy in the gray zone. First, the sudden shift from A- to E-effect in the SVV responses cannot by explained by the M-model. Second, at small and modest tilts, task execution is more or less automatic in contrast to the more demanding nature of the task (requiring more conscious effort) at large tilts. Third, errors in the SVV settings in the white zone cannot be explained by errors in perceived body tilt (Fig. 5*A*) but after the sudden decay of the A-effect there is a close resemblance (Figs. 5*B* and 6*B*).

These considerations led us to propose a dual-mechanism model (DM-model) for the subjective vertical incorporating: *1*) A default mechanism (system 1), operating according to the mathematical formulation of the M-model, whose signal is always available but may be ignored if the second system comes into play. We do not exclude that, in addition to the otoliths, somatosensory signals may also be involved (see Bronstein 1999; Howard 1982, 1986). Similarly, use of the M-model is not meant to rule out that system 1 may actually rely on the Bayesian approach proposed by Eggert (1998). *2*) A second, probably more cognitive mechanism, whose SVV settings are based on perceived body tilt, or on a shared underlying mechanism, without intervention of the idiotropic vector. This mechanism (system 2) can take over at large tilts when summoned into action. We have refrained from modeling the process that gives rise to the perceived body-tilt signal. To what extent it is determined by contributions of the otoliths, the canals, the somatosensory system, and graviceptors in the body is a separate problem, beyond the scope of the present study. The crucial assumption here is that perceived body tilt, whatever its basis, can be used in the SVV task at large tilt.

To allow simulations with this model, it was necessary to extract a predictor for the second system, based on the body-tilt estimates in the gray tilt zone. Because these responses are very noisy, we used a linear approximation to characterize their tilt-angle dependence. To keep the model simple, and since hysteresis effects in the gray zone were modest (Fig. 4*F*), the linear regression was applied on pooled CW and CCW data in the gray zone. The relation between errors in body-tilt estimates and tilt angle was significant ($r = 0.37$; $P = 0.0001$; $n = 103$) with a slope of 0.25 ± 0.07 and an offset of $-47 \pm 12°$. This means that the offset at $\rho = 180°$ is very small ($-2°$).

Based on this result, the following relation between the SVV and tilt angle (ρ) was attributed to the second mechanism

$$\beta = 0.75 \cdot \rho + 47 \qquad (2)$$

This relation is expressed in angle β ($\beta = \rho - \gamma$, see Fig. 2) instead of γ because the error γ is not a signal that is available to the system. *Equation 2* assumes that there is a one-to-one relationship between SBT and SVV in the gray zone, but it should be noticed that this is an approximation (see Fig. 6).

The formulation of the DM-model, so far, remained intentionally vague on the precise tilt angle demarcating the working range of the two systems. This critical tilt angle (ρ_c), assumed to be identical for leftward and rightward tilts, was a free parameter in the model. The parameters of the first system were those of the M-model. Accordingly, the DM-model has three free parameters (M, S, and ρ_c).

The fit procedure (see METHODS) minimized the total sum of squares of the vertical distances separating the data points from the DM-model prediction. The latter was based on the combination of the two system equations that were operative in system-specific adjacent tilt ranges, separated by the boundary at ρ_c. *Equation 1* (M-model) was applied in the range of absolute tilts from $\rho = 0°$ to $\rho = \rho_c$ and *Eq. 2* (2nd system) was used elsewhere. *Equation 2*, which has no free parameter, was not fitted but imposed. The optimal parameters (ρ_c, M, and S) were found by minimizing the total sum of squares for the combined model.

The best-fit result of the DM-model is shown in Fig. 7*B* where the white and gray zone now indicate the working ranges of the first and second mechanisms, respectively. Best-fit parameters values are shown in Table 1. The best-fit value for the critical tilt angle ($\rho_c = 133 \pm 2°$) is statistically indistinguishable from the white-gray demarcation, set by eye, that was used for descriptive purposes in earlier figures. The overall goodness of fit ($R^2 = 0.55$) is a dramatic improvement compared with the single-mechanism model result in Fig. 7*A*.

Now that the M-model (in the role of system 1) has been relieved of the impossible requirement of fitting data across the entire range, the fit in the white zone is much better. The best-fit values for its parameters ($M = 0.33 \pm 0.02$; $S = 0.58 \pm 0.03$) are in the expected range needed to account for the observed A-effect.

The most spectacular improvement in model performance is manifest in the gray zone where the second mechanism now provides a qualitatively correct explanation of the E-effect in SVV settings. In a quantitative sense, the model is clearly not perfect. Why the E-effect tends to be larger than the second mechanism predicts remains unclear.

WHAT DETERMINES THE SWITCH BETWEEN SYSTEMS? The dashed line in Fig. 7*B*, which indicates the predicted response of the default system if system 2 had not taken over, vividly illustrates a major conflict between the two systems near the tilt range where they change command (at the white-gray border). The question arises what may trigger the second system into action. We propose that as long as system 1 provides a strong and credible signal (more on this shortly), this is taken for granted and used in the SVV task, without bothering whether perceived body tilt would suggest a different response. In other words, the second system is not involved at all as long as the default system has a firm proposal. This explains why SVV settings are on average veridical after a 360° rotation back to upright, without conscious awareness of conflict, even though reliance on perceived body tilt would suggest a different setting (see Fig. 5). If the second system is not constantly monitoring whether the responses proposed by the default system are compatible with perceived body tilt, the sign that it should come into action has to be derived from the default signal. Which characteristics of the default signal could provide this clue?

As tilt angle increases, the signal from the default system, based on vector addition, becomes weaker because the head-directed idiotropic and the otolith signal point in widely different directions (see Fig. 1*B*). This decrease in signal strength will increase with tilt angle and be more marked if the idiotropic is strong. Based on an *M*-value of 0.4, rotation from 0 to 180° will cause a 57% smaller and more noisy net signal (the sum vector). A marked increase in noise level of SVV responses with tilt angle has been reported in previous experiments (Van Beuzekom and Van Gisbergen 2000). In addition to this deterioration of signal strength, an even more undesirable effect of the idiotropic at large tilts, further undermining the trustworthiness of the default system, is that it causes large systematic errors (A-effect).

Our data suggest that the critical threshold for abandoning the computational strategy based on the idiotropic is reached when the default system suggests a line setting perpendicular to the body axis. To illustrate this, we have plotted luminous-line orientation relative to the body (β, see also Fig. 2, *A* and *B*) as a function of tilt angle in Fig. 8. The SVV task requires that subjects adjust the line according to the rule $\beta = \rho$, as indicated by the dashed line. In the white zones, line settings deviate from veridical as if subjects underestimate their body tilt (A-effect). The sudden transition to the different response mode occurs near 135° tilt where the default system, indicated by the curved line, proposes a β-value that would actually be appropriate for a 90° real body tilt (see Fig. 8, *inset*). Based on the best-fit value for the idiotropic ($M = 0.33$), this would imply that switching occurs when the default system signal has lost 34% of its maximum strength.

If the $\beta = 90°$ criterion is generally valid, one would expect subjects with larger A-effect to have larger critical tilt angles. Data from individual subjects were insufficient to allow firm conclusions, but inspection of the data suggests that such a relation may exist.

This preliminary account suggests that the working range of the default system is limited by the characteristics of its own signal according to the rule that only proposals for β-settings $\leq 90°$ will be implemented. Proposals beyond this range are ignored and trigger the second system into action. Letting the
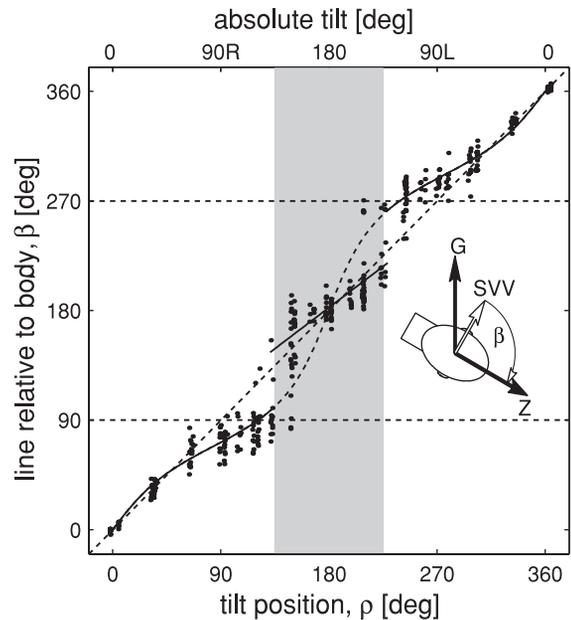

FIG. 8. Possible trigger criterion for activating second system. Data points show line settings in body coordinates (β) as a function of tilt angle ρ. Correct execution of SVV task ($\beta = \rho$) is indicated by the unity-slope dashed line. The curved line in the white tilt zone denotes settings proposed by the default system (same parameters as in Fig. 7*B*). Short line in gray zone represents predicted settings of second mechanism based on perceived body tilt. According to the hypothesis outlined in the text (see *Modeling results*), the change in response mode at white-gray border is triggered when β proposed by the default system exceeds 90° (see *inset*). G, direction of physical vertical; Z, *z*-axis of body; SVV, direction of subjective visual vertical setting proposed by mechanism 1.

default system provide the watch-dog signal frees the second system from the burden of constant monitoring, allowing it the more passive role of coming into action when summoned. To explain the impression in subjects that several settings are possible at large tilt, we suggest that the default signal, even if overruled, is always available. This may also help to explain why the take-over by the second system does not always occur.

If intervention by the second system serves to prevent excessive errors by the default system, there would be no need for this scenario when the idiotropic is small. Recent studies by Jaggi-Schwarz and coworkers (Jaggi-Schwarz and Hess 2003; Jaggi-Schwarz et al. 2003) have shown that application of a rotation paradigm designed to activate the canals leads to better performance in the SVV task, suggesting minimal involvement of the idiotropic vector. Because these studies were limited to tilts $\leq 90°$, results for the near-inverted tilt range are not available. To follow up on this work, it would be interesting to assess performance and to check for hysteresis effects in the subjective vertical task across the entire tilt range under dynamic conditions that allow the canal input to express itself. The relatively slow rotation at constant velocity and the waiting period in the present experiments must have limited these effects.

Because the second system seems to result in smaller systematic errors for the majority of tested tilt positions, compared with the default system, the question remains why it is not used throughout the entire range. Two possible factors may be considered. As already stated, the second system probably has a cognitive origin. The default system, which is more automatic, relieves the brain from this cognitive load in the normal

range of tilt angles. A second point is that scatter in the SBT results is considerably larger than in the SVV results, for all tilt positions (see Fig. 4). Therefore always relying on the second system would increase scatter in the SVV at small tilts.

Conclusion

In the normal working range, we provide new evidence in support of previous reports that there is a clear dissociation between performance in the subjective-vertical task and the sense of body tilt, compatible with the role of the idiotropic vector in the former but not in the latter. At large tilts, both spatial-orientation tasks appear to rely on the same processing of body-tilt signals with no role for the idiotropic. We suggest that this dichotomy reflects the involvement of two systems in external space perception, dedicated to different tilt domains: a default system conforming to Mittelstaedt's idiotropic-vector model and a more cognitive system, relying on perceived body tilt or on the same underlying mechanism, that becomes active at large tilt where the computational approach of the default system is inadequate.

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